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Underwater oviposition behaviour in two species of *Euphaea* in Borneo and Hong Kong (Odonata: Euphaeidae)

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Abstract

Submerged oviposition behaviour by female *Euphaea decorata* and *E. subcostalis* is reported. *E. decorata* descended to within 10 cm of the stream bottom and oviposited endophytically for a total of 59 min. An *E. subcostalis* female descended 3 cm to dead leaves at the stream bottom and stayed submerged for 20-25 s. Non-contact guarding by the male was observed in both cases. Submerged oviposition into substrates near to the stream bottom may be common behaviour for members of the Euphaeidae.

Introduction

Records of oviposition behaviour by members of the Euphaeidae (Calopterygoidea) are scarce in the published literature; indeed, it seems likely that ovipositing euphaeids are not commonly observed (Silsby 2001). Little mention of this family is made in the review of such behaviour given by Corbet (1999: 30-33), although the latter does cite Heymer's (1975) description of underwater oviposition by *Epallage fatime* (Charpentier), including partial submergence by the male.

The Oriental genus *Euphaea* is the largest genus in the family, containing 31 species (Schorr et al. 2005), of which the majority occur in southeast Asia, Indo-China or southern China (Tsuda 2000). A single species, *E. splendens* Hagen in Selys, is found in Sri Lanka, where it is endemic, while *E. yayeyamana* Matsumura & Oguma in Oguma is endemic to Japan, albeit confined to the Ryukyus in the southernmost part of the Japanese archipelago (Sugimura et al. 2001). Species are generally associated with well-wooded running waters. Very little is known about their oviposition habits, although underwater oviposition has been reported in three species: *E. ameeka* Van Tol & Norma-Rashid (Thompson 1998), *E. formosa* Hagen in Selys (Wang 2000) and *E. impar* Selys (Choong 2005), while unsubmerged oviposition has been reported for *E. ochracea* Selys (Wilson 2001).

How widespread is underwater oviposition in *Euphaea*, and how is it achieved? Is it an obligate or facultative behaviour in the species that practice it? We present separate observations of underwater oviposition behaviour by the southern Chinese *E. decorata* Selys and the Bornean endemic *E. subcostalis* Selys, and review the published records of oviposition in the Euphaeidae in general and *Euphaea* in particular.

Observations

Euphaea decorata

On 8 June 2005 we visited a rocky hill stream at Ng Tung Chai in the New Territories of the Hong Kong Special Administrative Region, China. The stream was pristine and fast-flowing, descending steeply through a series of cascades and waterfalls in native secondary woodland, from an altitude of 700 m to 150 m. The maximum width of the stream was 8 m. The weather was overcast with occasional bright sunny intervals, low wind and no rain. *E. decorata* was very common along the lower sections, and we were at an altitude of 250 m when we observed the following behaviour.

At ca 20 min after noon solar time, a female *E. decorata* was seen to dive in flight into the water surface in the middle of the stream, in the lee of a large boulder where the current was much reduced, directly above a submerged aquatic macrophyte, *Acorus tatarinowii* (Acoraceae) with narrow, elongate leaves 1-2 cm wide and 10-30 cm long. The longest leaves reached to within 1 cm of the water surface. The plant was rooted on rock at a depth of 10 cm, and the stream depth was ca 20 cm. After penetrating the water head first, the insect commenced a gradual descent from just below the water surface (Fig. 1) to a maximum depth of 10 cm, crawling along a leaf blade. Complete submergence was achieved within 30 s. For 38 min the insect crawled along several submerged leaf blades, repeatedly inserting its ovipositor into leaf tissue (Plate VIa). The female's body was variously orientated upright, sideways, or upside down as it manoeuvred amongst the leaf blades.

Figure 1: Female *Euphaea decorata* commencing submergence in stream at Ng Tung Chai, Hong Kong. The female entered the water in flight and descended to a depth of ca 10 cm, along a submerged leaf blade. Photo by G.T. Reels.

The insect then ascended to the surface along a leaf blade, and floated on its side at the surface for 20 s, whilst retaining contact with the leaf blade, presumably to replenish its air supply, prior to descending again in a similar manner. It then resumed its underwater crawling and ovipositing behaviour amongst the leaves of the plant for a further 15 min, and then again crawled to the surface up a leaf blade and exposed its thorax, but this time the exposure lasted for only 5 s, and the insect did not float on its side. It then re-submerged to resume oviposition for a further 6 min. Almost exactly 1 h after its original descent, the female again ascended, floated at the surface for a period of 80 s (Fig. 2), during which she appeared to be struggling to free herself from the water, and then took flight. Immediately she became airborne, i.e., within one second, a male *E. decorata* intercepted her, and the pair formed a wheel. This male, who had presumably fertilized the female's recently-oviposited eggs, had been perched on a boulder within 50 cm of the submerged female since her initial descent one hour earlier, in spite of the continued presence of a human observer 1 m away during the same period. The male had occasionally been forced to fly away when startled by the observers, or to drive away other males, but never flew more than 2 m from the submerged female, and had invariably returned to its favoured perch within 50 cm of the female after a few seconds. The pair subsequently stayed within 4 m of the oviposition site, and were perched in copula on a boulder 3 m away when we left the site some 5 min later.

Euphaea subcostalis

On 6 June 2004 we visited a shallow, pebbly, low gradient stream near to Deer Cave at the edge of the Melinau Limestone Formation at Gunung Mulu National Park in eastern Sarawak, Malaysia. The stream was pristine, running through alluvial forest at an altitude of ca 40 m, and was here characterised by shallow riffles alternating with deeper stretches, with a maximum width of 6 m. The weather was bright and sunny, with no discernible wind. *E. subcostalis* was common at the stream.

At ca noon solar time, a pair of *E. subcostalis* in the wheel landed on a stone protruding above the water in the mid-stream in a shallow riffle by which we were seated. Immediately after breaking tandem the female dove underwater beside the stone to a depth of 1-2 cm and began making oviposition movements into dead leaves (Plate VIb) whilst continuing to move deeper, reaching the stream bed, ca 3 cm deep at this point, before emerging after 20-25 s. Upon emergence she perched on another stone within 30 cm of the first. The male, who had remained on the original stone throughout the female's submergence, now joined the female, placing himself almost opposite her at a slight angle, and ca 2 cm away (Fig. 3), for ca 2 min until accidentally disturbed by one of the authors. Both insects then flew off and out of sight.

Climatic and stream conditions at the observation sites

The climate at Gunung Mulu National Park, as in Sarawak in general, is almost aseasonal, with rainfall spread throughout the year, and only a weak dry season during the southwest monsoon in August and September (Hazebroek & Morshidi 2001). However annual rainfall at Gunung Mulu is higher than in surrounding

areas of Sarawak. Water levels in streams and rivers are subject to large fluctuations throughout the year, and occasionally dry up for brief periods in the southwest monsoon, although torrential rain fall can also occur during this period. At the time the observations were made there had not been any heavy rainfall upstream for several days and water levels were at about their average levels.

In contrast to the situation in Sarawak, the climate in Hong Kong is strongly seasonal, with a warm wet southwest monsoon from May to September alternating with a cool, dry northeast monsoon from November to February, with transitional periods in between (Dudgeon & Corlett 2004). Streams regularly experience spate events in the wet season, and are subject to drastic declines in discharge by the end of the dry season. Water levels were high at the time of the observations reported above.

Euphaea decorata is known to have a univoltine, seasonal life cycle in Hong Kong (Dudgeon 1989), with a flight season corresponding broadly with the wet season. We have no data on voltinism in *E. subcostalis* in Sarawak, but the available evidence suggests that the species is on the wing year round, as might be expected given the almost aseasonal climate; a search of literature records and material collected by the authors during 2005 and 2006 reveals records of the species from all months except for May and December. The lack of records from these months is almost certainly due to lack of collecting effort in suitable habitats in May and December, in any case there is no correlation with the drier southwest monsoon period.

Figure 2: Female *Euphaea decorata* floating at surface after underwater oviposition into leaf blades of *Acorus tatarinowii*. The female floated for 80 s before taking flight from the water's surface. Photo by G.T. Reels.

Discussion

Completely submerged oviposition has been reported for many species of Zygoptera in several families, including Calopterygidae, Euphaeidae, Lestidae, Coenagrionidae and Platycnemididae, while a single family, Aeshnidae, contains the very few representatives of Anisoptera which are known to oviposit underwater (Corbet 1999, and references therein). It has been regarded as a behaviour restricted to species which oviposit endophytically (Corbet 1999), most frequently in lentic habitats, although Hawking et al. (2004) reported an observation of the Australian aeshnid *Notoaeschna sagittata* (Martin) ovipositing on bare rock, which is also the larval habitat, in a fast-flowing river whilst completely submerged. Benefits of this rather hazardous behaviour may include reduced male harassment while ovipositing, for species in which male densities at the water are relatively high, e.g., *Calopteryx dimidiata* Burmeister (Corbet 1999), reduced risk of female mortality from predation by aerial or surface predators, and enhanced survivorship of the prolarva and first larval stadium due to the placement of eggs at, or in close proximity to, the ultimate larval habitat. Such presumed benefits are, however, achieved at the cost of higher risk of female mortality due to drowning, particularly in lotic environments, or predation by aquatic organisms, although such a cost may be offset to some extent by male contact guarding.

With regard to the Euphaeidae, a variety of oviposition modes have been observed. Lieftinck (1948) recorded submerged oviposition by *Dysphaea dimidiata* Selys, with a maximum duration of over 45 min and non-contact guarding by the male. The insects arrived at the oviposition site in tandem. The female probed the substrate (bark) with her ovipositor before being released by the male, and then backed into the water. Orr (2003) described oviposition by *D. dimidiata* in which the female submerged on a log to a depth of 20 cm, remaining there for several minutes before re-surfacing and promptly forming a new tandem with the guarding male. Fraser (1934) mentioned oviposition in *Bayadera* and *Anisopleura* species without stating exactly where and how it is performed, although the Taiwanese *B. brevicauda brevicauda* Fraser apparently oviposits on moss-covered stones or on fallen leaves, and has been observed doing so some distance from water (Wang 2000). On 26 June 2000, Keith Wilson and GR observed a female *B. melanopteryx* Ris ovipositing into the underside of a log, hanging ca 40 cm above the surface of the water, at a hill stream pool at Ba Bao Shan, southern Hunan Province, China.

Within the genus *Euphaea*, most records of oviposition have involved submergence of the female. In addition to our own observations of *E. decorata* and *E. subcostalis*, Choong (2005) made the remarkable observation in Peninsula Malaysia of an unattended female *E. impar* hovering ca 20 cm above the water's surface in a fast-flowing stream, facing upstream, before it dived head-first into the water, descending to the stream bottom, at 5-10 cm depth, and ovipositing on slime-covered rocks and roots for 30 min before letting go of the substrate and rapidly rising to the surface. In the Taiwanese endemic species *E. formosa*, complete submergence during oviposition appears to be well-known and has been reported by various authors including Zhang & Wang (1997), Wang (2000) and Cao (2005). Wang (2000) identified two modes of oviposition in this species: one in which the female dives unattended and oviposits onto epilithic algae, and a second in which the male and female dive in tandem, ovipositing into unspecified substrates.

Zhang & Wang (1997) stated that such periods of submergence are brief, but Cao (2005), without elaborating on the precise duration, noted that the female may occasionally remain submerged for "a long time". Very brief periods of submergence and apparent oviposition, as in our observation of *E. subcostalis*, are best interpreted as either exploratory behaviour, or failed oviposition attempts, as discussed by Martens (1992). Wilson (2001), however, provided a photograph of a female *E. ochracea* ovipositing into a log in the splash zone of a torrential stream at Khao Phanom Bencha Forest in Thailand, with a non-contact guarding male in attendance. The female in Wilson's photograph was subject to frequent inundation, but presumably not completely submerged for more than a few seconds at a time. Contact guarding by male euphaeids has been reported for *Epallage fatime* (Heymer 1975) and *Euphaea formosa* (Wang 2000), but was not observed by the authors in *E. subcostalis* or *E. decorata*, even though males of these species often occur in high densities at the breeding sites, and was also not reported for *E. ameeka* by Thompson (1998) or for *E. impar* by Choong (2005).

There is evidence that underwater oviposition is a facultative behaviour in at least some species of *Euphaea*. Orr (2003) stated that species of this genus occurring on the large southeast Asian island of Borneo oviposit in submerged wood in streams, but has not seen female submergence in the two species, *E. ameeka* and *E. subcostalis*, for which he has oviposition observations (A.G. Orr pers. comm.). Our observations of *E. subcostalis* show that this species is capable of submerging, however briefly, while Thompson (1998), describing the reproductive behaviour of *E. ameeka*, noted that this species can also submerge, and gave an example of a female ovipositing underwater for 37 min and 42 s.

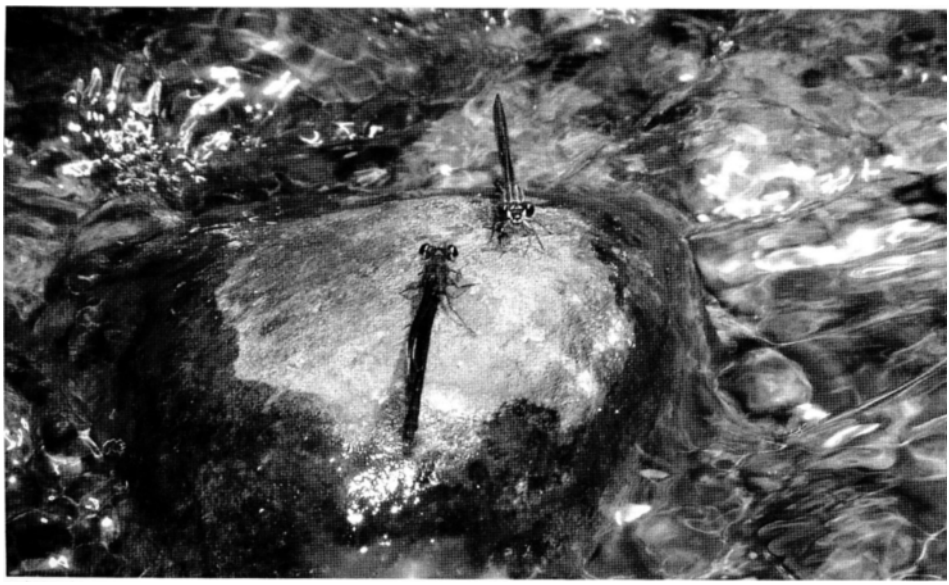

Figure 3: Female *Euphaea subcostalis* joined by non-contact guarding male upon emergence from water. The male had been present nearby during the female's submergence. Photo by R.A. Dow.

A study of the respiratory mechanism during underwater oviposition in *Calopteryx cornelia* Selys and other Asian calopterygids was recently conducted by Tsubaki (2006). Tsubaki found a significant association of regular submerged oviposition behaviour with the presence of dense bristles on the proximal costal area of the females' wings, suggesting a structural mechanism for trapping air to facilitate underwater respiration. Such bristles were absent or sparse in ten calopterygid species that oviposit underwater only occasionally or not at all (Tsubaki 2006). Dense bristles that may fulfill a similar function are present on the thorax (but not the wings) of the American *C. dimidiata* (Y. Tsubaki pers. comm.). We have examined females of four species of *Euphaea*: *E. decorata*, *E. impar*, *E. subcostalis* and the Hainanese endemic *E. ornata* (Campion), the first three of which are definitely known to oviposit underwater, at least facultatively, and found that wing bristles are either very sparse or absent in these species. In the first three species rapid entry into the water in flight has been observed. It may be postulated that, under such conditions of entry, fine bristles do not trap air effectively.

Interestingly, our record of *E. decorata* ovipositing endophytically into *Acorus* appears to be the only record of a euphaeid ovipositing into living green vascular plant tissue. As noted above, oviposition substrates known to be chosen by euphaeids include logs – overhanging, emergent or submerged, mosses, and submerged roots, twigs, dead leaves or epilithic algae.

In the case of *E. decorata*, further study of its oviposition behaviour to determine whether submerged endophytic oviposition is obligate or facultative would be instructive. If facultative, it would be interesting to determine which factor or factors govern the switch to completely submerged oviposition. Such a study would be relatively straightforward in Hong Kong, where the habitats are easily accessible and where the absence of other euphaeids removes the danger of confusion with females of different species.

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